

Original Study

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Rediscovery of an extinct species of caviine rodent of the Late Pleistocene after the Last Glacial Maximum in the Pampasic Domain (Argentina)

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Abstract: *Galea tixiensis* Quintana 2001, an extinct caviid species whose taxonomic status was questioned, has been identified at the Salto de Piedra (SPPL) paleontological site in Buenos Aires Province (Argentina). Morphological and morphometric analyses of these SPPL remains, together with contemporary and type locality specimens, support the taxonomic validity of this species. This identification dates the species back to ~16,300 cal BP and extends its geographic distribution ~200 km eastward in the Pampasic Domain. Other caviine include the extinct *Microcavia* cf. *M. robusta*. Paleoenvironmental correlations suggest that this diverse caviine fauna likely correspond to climatic and ecological shifts during the Pleistocene-Holocene transition. Species like *M. robusta* and *Galea ortodonta* disappeared as grasslands replaced shrub steppes in the region during the Holocene, and *Cavia aperea* arrived here from the north. Today, *C. aperea* is the only caviine species inhabiting the core of the Pampasic Domain, *Microcavia australis* and *Galea leucoblephara* remain restricted to southern xeric

coastal environments and *G. tixiensis* appears to have become extinct in the 19th century. This study provides valuable insights into faunal shifts within the Pampasic Domain, linking these findings to broader patterns of Late Pleistocene biodiversity and environmental dynamics in South America.

Keywords: *Galea tixiensis*; *Microcavia robusta*; zoogeography; extinction

1 Introduction

The subfamily Caviinae is a diverse South American group of small Caviidae rodents, represented by three extant genera (*Cavia*, *Galea*, and *Microcavia*) and five extinct genera (*Dolicavia*, *Neocavia*, *Orocavia*, *Orthomyctera* and *Palaeocavia*). These genera have a complex taxonomic history, diversity, and evolutionary record, well represented in central and northern Argentina since the Late Miocene (Dunnum 2015; Madozzo-Jaén and Pérez 2024; Madozzo-Jaén et al. 2018; Verzi and Quintana 2005). The extant genera include multiple living species, as well as some extinct species from the Late Neogene and Quaternary periods of South America, particularly abundant in the Pampasic Domain (e.g., Quintana 1996, 1998, 2001; Tonni et al. 1988; Verzi and Quintana 2005).

The evolutionary divergence of species from the genus *Galea* appears to have occurred during the Pliocene (Bezerra 2008; Dunnum and Salazar Bravo 2010), while the origin of *Microcavia* seems to date to the mid-Pliocene in the Pampasic Domain (e.g., Quintana 1996; Teta et al. 2017; Ubilla et al. 1999). The genus *Galea* Meyen, 1833, commonly known as the Yellow-toothed Cavy, includes two extinct – *Galea ortodonta* Ubilla and Rinderknecht, 2001 and *Galea tixiensis* Quintana, 2001 – and five extant – *Galea comes* Thomas, 1919, *Galea flavidens* (Brandt, 1835), *Galea leucoblephara* Burmeister, 1861, *Galea musteloides* Meyen, 1833 and *Galea spixii* (Wagler, 1831) – species of small, colonial and diurnal,

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terrestrial herbivores that inhabit open shrublands and grasslands exclusively in South America (Bezerra 2008; Cabrera 1953; Dunnum 2015; Francia et al. 2012). Among the currently recognized living species, *G. leucoblephara* is notable for inhabiting arid and semi-arid regions in central-western and southern Argentina, reaching the southern areas of Buenos Aires Province (Argentina) (Dunnum 2015; Massoia 1985; Pardiñas and Cenizo 2023; Reig 1964; Figure 1).

The extinct species, *G. ortodonta*, has been recorded from the Late Pleistocene of Uruguay and the Pleistocene of Bolivia. Another extinct species, *G. tixiensis*, was found in the Pampasic Domain, specifically within Holocene and historical sediments (Lujanian and Platan Stages/Ages) in the Tandilia hill system at the Cueva Tixi and Cueva El Abra archaeological sites in the eastern Pampasic Domain (e.g., Quintana 2001). *G. tixiensis* was later discovered in Late Pleistocene deposits (Lujanian Stage/Age) within the Paraná River basin at the Arroyo Toropí paleontological site, in the Subtropical Domain, western Corrientes Province of Argentina (Francia et al. 2012; Figure 1).

However, Teta and Campo (2017), using both qualitative and quantitative cranial characteristics of specimens from the three currently recognized subspecies of *G. leucoblephara*, suggested that *G. tixiensis* should be considered synonymous with *G. leucoblephara*. Nevertheless, other authors have pointed out that the lack of comprehensive studies on type specimens limits the ability to conclusively determine the taxonomic validity of this species (e.g., Hadler et al. 2024; Pardiñas and Cenizo 2023).

On the other hand, the genus *Microcavia* Gervais and Ameghino, 1880, known as the Mountain Cavy, includes four extinct and four extant species. Living species of *Microcavia* inhabit arid and semi-arid regions of Bolivia, western and southern Argentina, and Chile (Dunnum 2015). *Microcavia australis* (I. Geoffroy Saint-Hilaire and d'Orbigny, 1833) is the only extant species (like *G. leucoblephara*) that reaches the southern part of Buenos Aires Province (Dunnum 2015; Fernández et al. 2012; Figure 1). This species has also been found in Late Pleistocene and Holocene deposits within the Pampasic Domain (Quintana 1996). The four extinct species are *Microcavia chapalmalensis* Ameghino, 1908, associated with the Chapadmalalan Stage/Age (Early to Late Pliocene); *Microcavia reigi* Quintana, 1996, related to the Marplatense Stage/Age (Late Pliocene to Early Pleistocene); *Microcavia robusta* Gervais and Ameghino, 1880, linked to the Ensenadan Stage/Age (Early to Middle Pleistocene) and the Lujanian Stage/Age (Late Pleistocene to Early Holocene); and *Microcavia criollensis* Ubilla, Piñeiro, and Quintana, 1999, assigned to the Lujanian Age (Quintana 1996; Ubilla et al. 1999).

The taxonomic diversity of caviine rodents during the Late Pleistocene in the eastern Pampasic Domain, also

known as the Humid Pampas due to its higher rainfall, remains an open question, awaiting further findings that could help clarify existing taxonomic gaps. In this study, we examined the cranial and dental morphology of caviine rodents from Late Pleistocene sediments in Buenos Aires Province. Based on the findings of extinct and extant species of *Galea* and *Microcavia* that no longer inhabit the region, we discuss zoogeographical considerations in light of the paleoenvironmental conditions during the Late Pleistocene and the transition to the Early Holocene. For this purpose, we applied various morphometric analyses to explore similarities and differences between the extinct and extant species.

2 Regional settings

Fossil remains here analysed have been recovered within the Humid Pampa Subregion of the Pampean Region, largely overlapping with the boundaries of Buenos Aires Province. This subregion is a vast plain interrupted in the southeast by the Tandilia and Ventania hill systems. The area's climate is influenced by the Atlantic anticyclone, with an average annual temperature of approximately 18 °C and mean annual precipitation around 1,200 mm (Burgos 1968). This subtropical climate, combined with organic-rich surface soils, supports pseudo-steppe grasslands dominated by Poaceae genera, such as *Briza*, *Danthonia*, *Melica*, *Nassella*, *Piptochaetium*, and *Poa*, characteristic of the Southern Pampa phytogeographic unit (Oyarzabal et al. 2018). The influence of the ocean decreases from northeast to southwest, creating a progressively more arid climate in the southwestern area, where mean annual precipitation is around 600–800 mm and mean annual temperature is approximately 14 °C (Burgos 1968). Consequently, the vegetation gradually changes to arid steppes with more xeric shrubs and trees typical of the Espinal and Monte phytogeographic units (Oyarzabal et al. 2018).

Zoogeographically, the grassland covering most of the Humid Pampas is part of the Pampasic Domain of the Guyano-Brazilian Subregion within the Neotropical Region (Ringuelet 1955, 1961). This Domain includes Buenos Aires Province (except the south) and parts of neighbouring Córdoba, Santa Fé, and La Pampa Provinces (Figure 1). The Pampasic Domain acts as a large ecotone between the Subtropical Domain (Guyano-Brazilian Subregion) to the north, the Central or Subandean Domain (Andean-Patagonian Subregion) to the west and south, and the Patagonian Domain (Andean-Patagonian Subregion) to the south. Currently, Brazilian or Subtropical fauna, with no endemic



Figure 1: Map of the Southern Cone of South America with the location of the studied sites in the Pampasic Domain (*sensu* Ringuelet 1955, 1961), the current distribution of *Galea leucoblephara* and *Microcavia australis* and the upper part of the stratigraphic sequence of Salto de Piedra site (black star). The colored dots referred to the different caviine species recovered in the fossil sites. Localities mentioned in the text: 1. Bahía Blanca; 2. Oriente; 3. Miramar; 4. Camet Norte; 5. El Abra and Cueva Tixi; 6. Libertad or Dolores Fm; 7. Sopas Fm; 8. Arroyo Toropí; 9. Salto de Piedra (this work).

species (Ringuelet 1955, 1961), characterize the Pampasic Domain.

However, during Quaternary cold-dry climatic phases, such as the Last Glacial Maximum (LGM, 26,000–18,000 BP), the Antarctic Cold Reversal (ACR, 14,700–13,000 BP), or the Little Ice Age (LIA, 1,300–1,900 AD), the range of Subtropical faunas contracted, allowing the expansion and interconnection of Patagonian and Sub-Andean faunas. During warm-wet phases, such as the Holocene Climate Optimum (HCO, 7,500–4,500 BP) or the Medieval Climatic Anomaly (MCA, 800–1,300 AD), the opposite occurred, enabling the spread of Subtropical faunas (Tonni 2017).

3 Materials and methods

3.1 Fossil sites and study samples

The new caviine remains presented in this work come from Salto de Piedra (SPPL) open-air paleontological site (upper basin of Tapalqué Creek (36°56'54.6" S, 60°22'19.9" W; 173 m asl) in Buenos Aires Province, Argentina (see Figure 1). This small valley is carved into Plio-Pleistocene loessic sediments that intermittently outcrop along the creek banks. The surrounding interfluvies are covered by a layer of Late Pleistocene and Holocene eolian deposits, which serve as the parent material for most of the region's present-day soils (Favier-Dubois et al. 2021; Prado et al. 2019). The site has been systematically excavated using 3D Total Station coordinates, within two specific areas along the river-banks of the Tapalqué Creek: Section I downstream and Section II upstream (Favier-Dubois et al. 2021; Prado et al. 2019). Based on stratigraphic and sedimentological analyses, Favier-Dubois et al. (2021) divided the sedimentary sequence into six depositional allounits (U) separated by erosive unconformities and identified 12 facies (F), each with distinct sedimentary and taphonomic characteristics (Figure 1, top of the sequence). These allounits, labelled from U1 to U6, are summarized in the Supplementary Material.

They are broadly correlated with the Upper Pampean (U1), Lujanian (U2 to U5), and La Postrera (U6) Formations (Favier-Dubois et al. 2021; Prado et al. 2019, 2024). The fossil samples analysed in this study were recovered from U4 (F7–F9) within the Guerrero Member of the Lujanian Formation. This unit has been dated to the post-LGM period near the Pleistocene-Holocene transition using radiocarbon methods (Table 1).

The *Galea* specimens recovered were notably larger than the present-day *G. leucoblephara* species. Thus, our fossil remains were compared with *Galea* specimens from Cueva Tixi (CT), where a larger species of the *Galea* group (*G. tixiensis*, Quintana 2001) was described for the Pampasic Domain.

Cueva Tixi (CT) is the type locality of *G. tixiensis* Quintana 2001. This is an archaeological cave site located in the La Vigilancia hills within the Tandilia hill system, composed of Paleozoic sedimentary rocks from the La Tinta Formation (37°57'48" W; 58°2'30" S; 190 m asl, Buenos Aires Province; see Figure 1). The cave is approximately 1.80 m in height and covers an area of about 50 m², opening onto a narrow valley through which a tributary of the San Pedro stream flows (Quintana 2001; Tonni et al. 1988). The site was discovered by Carbonari in the 1980s, who invited J.L. Prado to study the faunal assemblage recovered from the first test excavation. Initial reports based on earlier fossil sampling (Prado et al. 1985; Tonni et al. 1988) led to systematic excavations conducted under Diana Mazzanti's direction since the mid-1980s onwards. Our present study evaluates eight mandibles (four left and four right) from the first sampling at CT (Tonni et al. 1988) bearing partial dentition from *Galea* specimens. In their analysis, these authors examined 650 bone remains from 16 artificial 5-cm levels within a 1.5 × 1.5 m square, following the stratigraphic framework by Figini et al. (1985), who designated five natural strata with a total thickness of about 80 cm. Pardiñas (1999, 2000) later refined this chronostratigraphy, which is described in detail in the Supplementary material.

The faunal remains are distributed across four of these strata (b–e). Stratum e is divided into an upper (mid-Holocene)

Table 1: Radiocarbon dates obtained from F9, F8 and F7 facies of the U4 unit in Salto de Piedra palaeontological site.

Facies	Sample dated	Lab number	Dating method	Age BP	Reference	Calibrated years BP (2σ)
F9	Bone	GrA-49131	AMS	10140 ± 60	Prado et al. (2015)	11,920–11,3241
	Bone	PSUAMS 16314	AMS	11610 ± 60	Bellinzoni pers. com.	13,515–13,315
F8	Bone	PSUAMS 13960	AMS	12305 ± 45	Bellinzoni pers. com.	14,880–13800
	Bone	5095.1.1	AMS	13329 ± 60	Prado et al. (2024)	16,195–15,766
F7	Bone	PSUAMS 16313	AMS	13430 ± 70	Bellinzoni pers. com.	16,530–15,780
	Bone	GrA-47178	AMS	13590 ± 60	Prado et al. (2015)	16,581–16,151

PSUAMS, Pennsylvania State University AMS Radiocarbon Laboratory; GrA, Centre for Isotope Research in Groningen, AMS Radiocarbon Laboratory.

and lower (Pleistocene-Holocene boundary) section based on its chronological, archaeological, and faunal contexts (Figini et al. 1985). The *Galea* remains analysed here, from levels 4, 5 (stratum b), level 8 (stratum d), and levels 9–12 (upper stratum e), correspond to the mid-Holocene, Late Holocene, and historical periods (Supplementary Table S1).

Both, the *Galea* specimens from SPPL and CT, as well as *Microcavia*, are housed at the Instituto de Investigaciones Arqueológicas y Paleontológicas del Cuaternario Pampeano (INCUAPA) from the Facultad de Ciencias Sociales (FCS) of Universidad Nacional del Centro de la Provincia de Buenos Aires (UNICEN). To obtain a reliable reference collection for further comparisons, contemporary and archaeological specimens of the current species, *G. leucoblephara*, were also included. Present-day specimens come from Chaco, Córdoba, and La Pampa Provinces, and are housed at the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN, Buenos Aires) and at the Grupo de Estudios en Arqueometría, Facultad de Ingeniería (GEArq–FIUBA, Buenos Aires). Archaeological samples of *G. leucoblephara* come from the Agua de Mula (Mendoza Province), Gruta del Indio-Rincón del Atuel (Mendoza Province), and Cueva Huenul I (Neuquén Province) Late Holocene archaeological sites, all housed at GEARq–FIUBA (Supplementary Table S1).

Finally, *Microcavia* remains from SPPL were analysed and compared with molariform measurements of extinct *Microcavia* species (*M. robusta*, *M. chapalmensis* and *M. reigi*) extracted from the literature (Quintana 1996; Ubilla et al. 1999) and with present-day *M. australis* specimens from Neuquén Province (GEArq–FIUBA).

3.2 Methods

Calibration of radiocarbon ages from the study sites were obtained using OxCal with the SHCal20 calibration curve (2 σ cal BP), to provide the most probable time interval (Hogg et al. 2020).

The taxonomic nomenclature used for molariforms and mandibles of the caviid specimens here analysed follows that of Quintana (1996) and Madozzo-Jaén et al. (2018), respectively.

Four lower premolars (pm4) of *Galea* specimens recovered from SPPL were initially set aside due to their large size. In this sense, the lower premolar was selected as it was the only tooth available across all specimens, allowing for consistent morphometric and statistical comparisons. These samples, together with the *Galea* specimens recovered from CT, Late Holocene archaeological sites from Mendoza and present-day specimens, were photographed in occlusal view with a digital camera Leica DMC4500 installed on a binocular

stereomicroscope Leica S6D. For consistency, images of left premolars were used; when left premolars were not available, images of right premolars were mirrored prior to landmark placement. Premolar shape analysis was performed using two-dimensional (2D) geometric morphometrics, with eight landmarks placed at the points of maximum curvature on the salient and interior angles common to all specimens.

Landmark location was carried out using TPSdig2 v.2.32 (Rohlf 2006) (see Figure 2). To assess the repeatability of landmark positioning, each specimen was re-digitized five times. Measurement error was estimated through a MANOVA to verify that differences in landmark placement across specimens were not significant. Results confirmed high repeatability, with no significant differences found in landmark positions ($p = 0.999$).

Morphometric analyses were conducted using PAST software v. 4.16c (Hammer et al. 2001). As a preliminary step, the 2D landmark coordinates were scaled using general Procrustes analysis (GPA). Posteriorly, a linear discriminant analysis (LDA) was performed. LDA is commonly used for classifying data into predefined groups or categories, maximizing the separation between groups while minimizing variation within each group. Since our goal is to classify the SPPL specimens into known groups (Present Day, Late Holocene, and Cueva Tixi reference collections), we applied LDA to identify the features most useful for distinguishing between groups. To determine if the morphological differences indicated by the

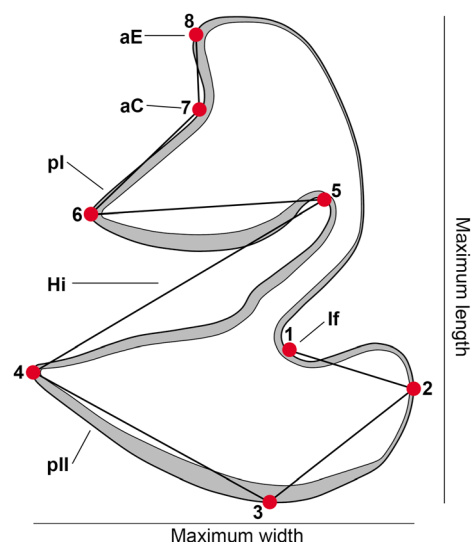


Figure 2: Scheme of the pm4 from *Galea* genus indicating the maximum width and length measurements and position of the eight landmarks used for capturing the shape of the teeth. The landmarks were positioned in areas easily distinguishable in all the pm4 analysed, amongst them the internal flexid (If), the anterior (pI) and posterior (pII) prism, the hypoflexid (Hi), the additional cleft (aC) and the additional extension (aE).

LDA between the reference collections were statistically significant, a MANOVA test was applied.

Measurements of the length and width of each pm4 were also taken (Figure 2, Supplementary Table S1). Differences in length and width were analysed using ANOVA, and the results were presented in boxplots and XY plots to classify the specimens in two-dimensional space, comparing length versus width.

4 Results and discussion

4.1 Systematic paleontology and comparative analysis

Order Rodentia Bowdich, 1821

Suborder Hystricomorpha Brandt, 1955

Infraorder Hystricognathi Tullberg, 1899

Superfamily Caviioidea Fischer de Waldheim, 1817

Family Caviidae Fischer de Waldheim, 1817

Subfamily Caviinae Fischer de Waldheim, 1817

Genus *Galea* Meyen, 1833

Galea tixiensis Quintana, 2001

Referred material: anterior fragment of left mandible, with complete premolar (pm4) recovered from U4-F7 (FCS-P.320). Anterior part of left mandible, with complete premolar (pm4), and fragments of first lower and second molars (m1, m2) recuperated from U4-F7 (FCS-P.321). One complete right isolated lower premolar recorded at U4-F7 (FCS-P.322). One complete left isolated lower premolar documented at U4-F7 (FCS-P.323).

Both anterior fragments of mandibles are robust, featuring a horizontal crest on its labial side that extends below the middle part of the pm4, along with a pronounced dorsal fossa (Figure 3A–D). These features are consistent with those described for the genus *Galea* by Kraglievich (1930), Cabrera (1953) and Contreras (1964). Additionally, the mandible exhibits a distinct ridge at the centre of the diastema, visible in dorsal view, and an oval-shaped mentonian foramen positioned immediately anterior to pm4, at the level of the lower part of the crest (Figure 3A). These characteristics are also present in the mandibles from CT specimens examined here (Figure 3E and F), as well as in *G. leucoblephara* (Cabrera 1953; Contreras 1964; Dunnum 2015). The robustness of the jaws appears more pronounced in the SPPL and CT specimens compared to *G. leucoblephara* (Figure 4G and H). In fact, Quintana (2001) pointed out that the difference between the two species lies in the fact that the skulls, mandibles, and molariforms of *G. tixiensis* are larger than those of *G. leucoblephara*. Therefore, size

appears to be the most prominent distinguishing variable between *G. leucoblephara* and *G. tixiensis*.

The pm4 found at SPPL and CT have a biprismatic lanceolate-shaped in occlusal view, being lingually convex and labially pointed (Figure 4A–F). It also features a large anteroposterior curved hypoflexid, filled with cement in the deeper area. These characteristics align with those of the *Galea* and *Palaeocavia* genera (Contreras 1964). In contrast, the *Cavia* genus exhibits hypoflexids filled with abundant cement, but the prisms are laminated (Quintana 1998; Verzi and Quintana 2005). The hypoflexid in *Microcavia* is not filled with cement (Quintana 1996). The enamel is interrupted around the lingual side, except in the internal or lingual flexid, as observed in other caviines (Madozzo-Jaén et al. 2018). In species of *Galea*, the posterior prism has a straight base and an internal flexid with a fold on the lingual side, appearing as a notch (Figure 4). The anterior prism exhibits a rounded additional extension, delimited by both, an additional and internal cleft (Figure 4A–B and E–F). This feature, although more attenuated, is also observed in the specimens of *G. tixiensis* examined here from CT (Figure 4C and D). Notably, this feature is rarely present in *G. leucoblephara* (Figure 4G and H). However, previous research has noted the intraspecific variability in the shape of the prism and additional extension, as well as for the configuration of flexids and clefts in the pm4 of populations of both *G. leucoblephara* (Contreras 1964) and *G. tixiensis* (Quintana 2001). In fact, Quintana (2001) pointed out that the molariforms of *G. tixiensis* fall within the same variability range observed for *G. leucoblephara*.

The LDA indicates a separation between the reference groups (Figure 5) and correctly classified the 88.24 % of the specimens by their shape. More specifically, the 87.5 % of PD specimens, the 100 % of CT specimens and the 84.2 % of LH specimens were correctly classified (Table 2, Supplementary Tables S2 and S3). The Axis 1 explains most of the variability (67.37 %) while Axis 2 explains the 32.63 % of the variability of the shape. CT and the majority of LH specimens are distributed along negative values of Axis 1, while most of the contemporary reference specimens are along positive values of the same axis. On the other hand, it is remarkable the separation of the LH specimens along the negative values of Axis 2. However, to test the significance of the differences observed in the LDA, a MANOVA test was applied to corroborate them. Results initially obtained from this test indicated significant differences (p -value = 0.003). Nonetheless, pairwise comparisons show that these differences are mostly due to the fact that CT and LH samples are morphologically different from PD ones (p -value < 0.02), but similar between them (CT vs. LH p -value = 0.221). These results indicate that archaeological samples are morphologically different from present-day ones. A possible explanation to

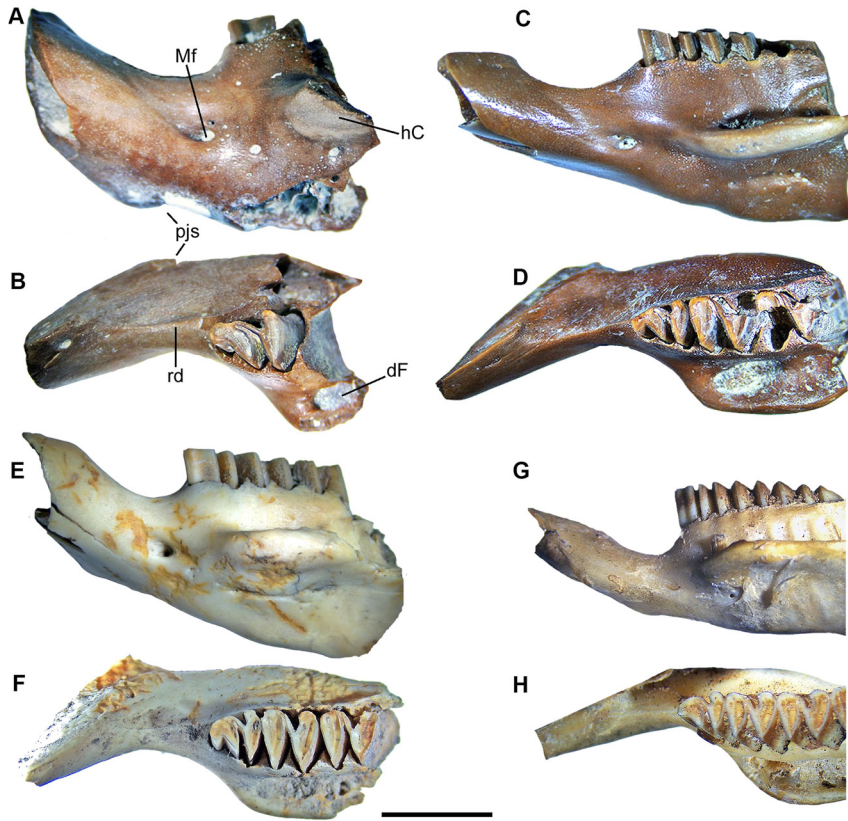


Figure 3: Mandibles of *Galea tixiensis* recovered from Salto de Piedra (SPPL) compared with *G. tixiensis* from Cueva Tixi (CT), and *Galea leucoblephara* from recent collection of La Pampa Province (GEArq-FIUBA, Buenos Aires city). (A-B) left mandibular fragment with pm4 assigned to *G. tixiensis* in lateral and frontal views (FCS-P.320, U4-F7); (C-D) left mandibular fragment with pm4, m1 and m2 assigned to *G. tixiensis* in lateral and frontal views (FCS-P.321, U4-F7); (E-F) left mandibular fragment with pm4, m1 and m2 of *G. tixiensis* in lateral and frontal views (CT *stratum b*); (G-H) left mandibular of modern *G. leucoblephara* in lateral and frontal views (La Pampa Province). Abbreviations: dF, dorsal fossa; hC, horizontal crest; Mf, mentonian foramen; pjs, posterior joint of the symphysis; rd, ridge of the diastema. Scales = 5 mm.

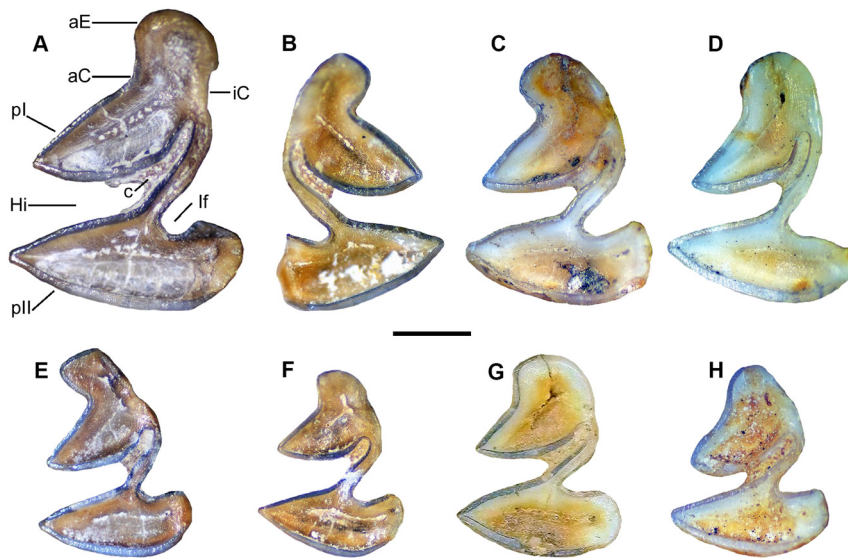


Figure 4: Oclusal views of lower premolars (pm4) of *Galea tixiensis* recovered from Salto de Piedra (SPPL) compared with *G. tixiensis* from Cueva Tixi (CT), *Galea leucoblephara* from Late Holocene (Agua de la Mula, Mendoza Province), and *G. leucoblephara* from recent collection of La Pampa Province (GEArq-FIUBA, Buenos Aires city). (A-B) left and right pm4 assigned to *G. tixiensis* (FCS-P.320, FCS-P.322, U4-F7); (C-D) left pm4 of *G. tixiensis* (CT *stratum b*); (E-F) left pm4 assigned to *G. tixiensis* (FCS-P.321, FCS-P.323, U4-F7); (G) left pm4 *G. leucoblephara* (Agua de la Mula); (H) left pm4 of modern *G. leucoblephara* (La Pampa Province). Abbreviations: aC, additional cleft; aE, additional extension; c, cement; Hi, hipoflexid; iC, internal cleft; If, internal flexid; pI, anterior prism; pII, posterior prism. Scales = 1 mm.

this fact could be related to environmental differences associated with the geographical location where samples were recovered. Nonetheless, phenotypic shifts between past and present samples could also be triggered by human influence on habitat and environment (Cucchi et al. 2014). Thus, it cannot be discarded that the variation in shape

morphology between the archaeological samples (LH and CT) and PD samples may respond to human causes such as agricultural activities. Further analyses with larger sample sizes should be done in this respect. Finally, although the LDA and MANOVA do not indicate significant morphological differences of the CT samples, *Galea* specimens recovered

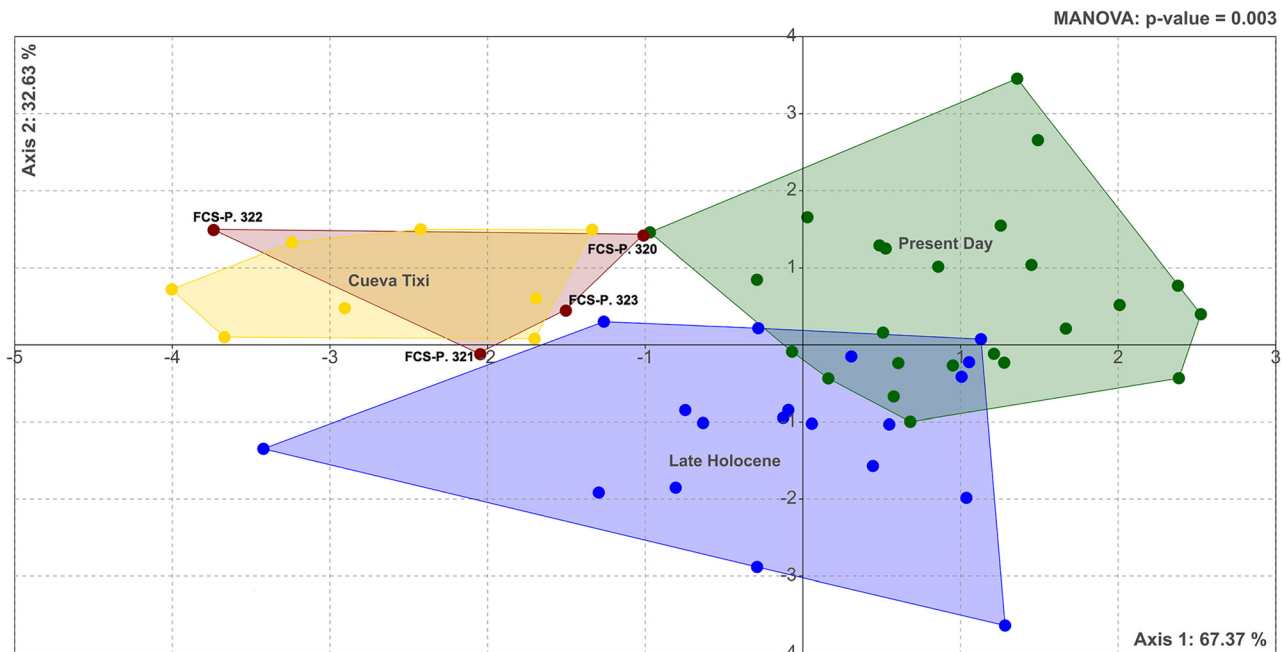


Figure 5: Linear discriminant analysis (LDA) results for each of the groups used as reference to compare with SPPL *Galea* specimens (red dots). Salto de Piedra samples: FCS-P. 321; FCS-P. 323; FCS-P. 322; FCS-P. 320.

Table 2: Reference samples classification within the groups established for the LDA.

	PD	CT	LH	% Correctly classified
PD	21	0	3	87.5
CT	0	8	0	100
LH	1	2	16	84.2
SPPL	0	4	0	–

Reference sample only includes LH (Late Holocene), PD (Present Day) and CT (Cueva Tixi) specimens with the purpose to obtain a statistically significant sample for further classifying Salto de Piedra (SPPL) specimens and evaluate their similarities and differences with the reference sample. Only two samples were incorrectly classified for the LH as PD samples, one sample was incorrectly classified as LH from PD specimens and all the specimens from CT were correctly classified.

from SPPL are classified as morphologically similar to CT (Table 1, Figure 5).

Regarding specimens size, ANOVA tests revealed significant differences in length measurements, while width measurements did not show notable differences. Specifically, PD and LH specimens were similar in length (p -value = 0.778) but differed significantly from CT specimens (LH vs. CT: p -value = 0.011; PD vs. CT: p -value = 0.030). Visual inspection through boxplots supports the ANOVA results, showing that CT and SPPL specimens generally exhibit greater average length values (Figure 6A). Notably, a potential bimodal distribution in CT specimens suggests the presence of two

phenotypes differing in size, likely representing *G. tixiensis* and *G. leucoblephara* (Figure 6A and C). In fact, two CT specimens fall within the smallest range for both length and width measurements (Figure 6C). However, a larger sample size could further clarify these distinctions.

For width values (Figure 6B), boxplots indicate no significant differences, though the bimodal distribution of CT specimens still apparent. Based on length measurements, SPPL specimens align more closely with CT samples; however, significant differences exist between these two groups and the PD and LH reference collections. Only one specimen from SPPL (FCS-P.323) falls among the lowest length values, while the FCS-P.320 specimen (Figure 6E) consistently ranks as the largest, regardless of length or width. Given the morphological and size similarities between CT and SPPL specimens, *Galea* remains from SPPL may be better assigned to *G. tixiensis* than to *G. leucoblephara*, with FCS-P.320 possibly representing the upper range of the phenotypic variability for the species. Overall, the measurements from this study suggest that both, SPPL and CT samples, exhibit larger length values compared to contemporary and Late Holocene *G. leucoblephara* remains (Figure 6).

In contrast, Teta and Campo (2017) found that the craniodental measurements of *G. tixiensis* fell within the variability range of *G. leucoblephara* when compared to numerous specimens from the three recognized subspecies: *G. l. leucoblephara* Burmeister, 1861; *G. l. demissa* Thomas, 1921; and *G. l. littoralis* Thomas, 1901. Unfortunately, these

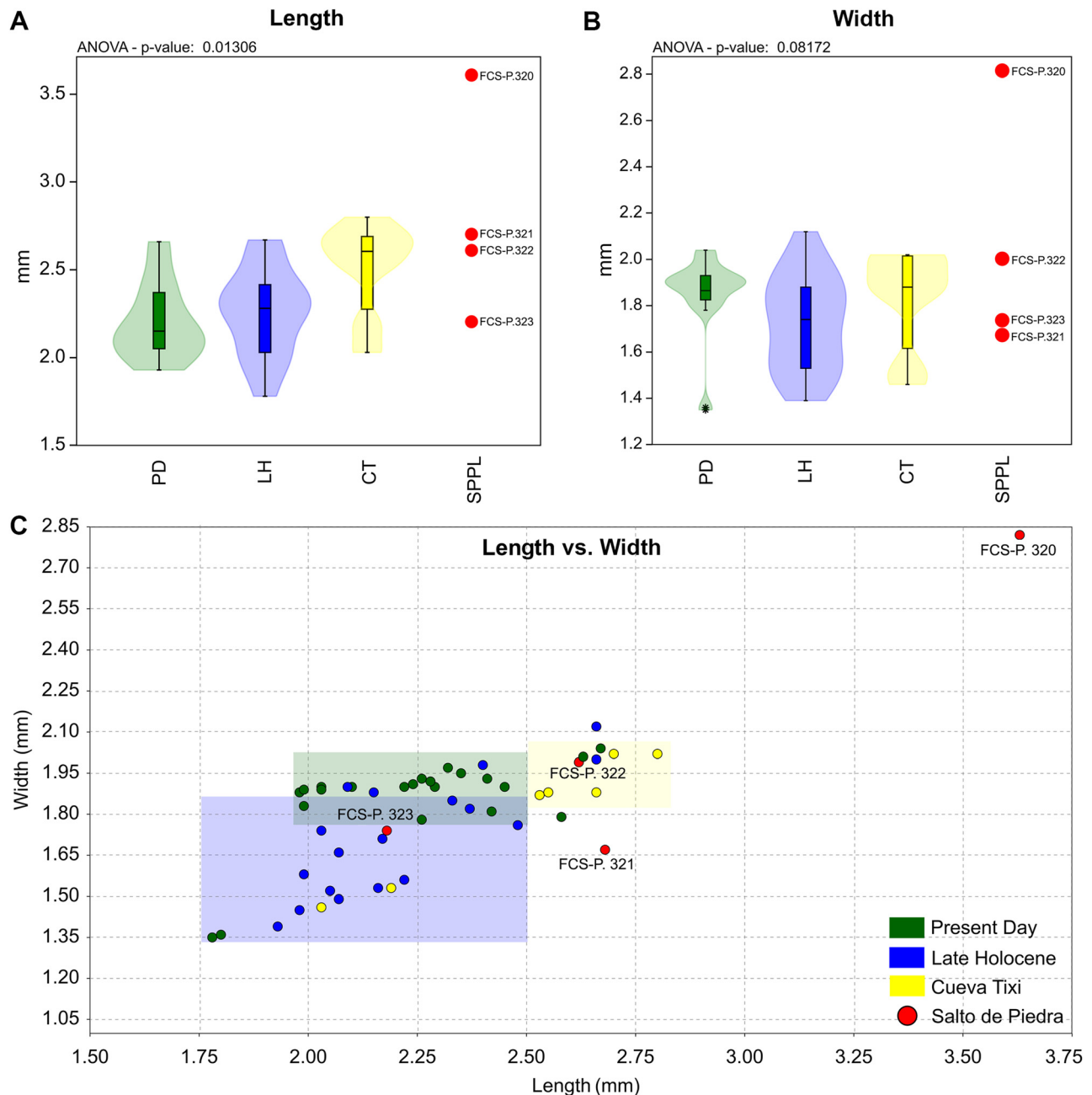


Figure 6: Graphic representation for length versus width values. (A) Violin and box plots for length and width showing the mean values and the 25 and 75 percentiles. (B) XY plot classifying all the specimens by their length and width. (C) Length vs. width measurements of Present Day, Late Holocene, Cueva Tixi and Salto de Piedra specimens. Note that the FCS-P. 320 SPPL specimen is clearly separated from the rest. ANOVA tests indicate that length values show significant differences between the reference groups, being the samples of Cueva Tixi (CT) different from the Present Day (PD) and Late Holocene (LH) ones. Salto de Piedra (FCS-P. 321; FCS-P. 323; FCS-P. 322; FCS-P. 320) samples are mostly classified as similar to CT specimens.

authors relied on digital measurements (using the software tpsdig2) based on photographs of the *G. tixiensis* holotype (taken by Bezerra 2008; Francia et al. 2012), as the curator of the Archaeology Laboratory of the Faculty of Humanities at the National University of Mar del Plata (Buenos Aires) declined to provide the holotype for its study (Teta and Campo 2017: 210, 213). Although we did not examine the

G. tixiensis holotype in this study, we were able to make comparisons with specimens recovered from the type locality (Cueva Tixi), collected by Tonni et al. (1988).

Genus *Microcavia* Gervais and Ameghino, 1880

Microcavia cf. *M. robusta* Gervais and Ameghino, 1880

Referred material: fragment of left maxilla without teeth recovered from U4-F7 (FCS-P.324). Complete left upper

first molar (M1) recorded at U4-F9 (FCS-P.328). Complete third molar (M3) found in U4-F7 (FCS-P.325). Complete left lower premolar (pm4) recovered from U4-F7 (FCS-P.326). Complete left lower first molar (m1) recorded at U4-F7 (FCS-P.327).

The fragmented maxilla recovered from SPPL shows the posterior edge of the incisive foramina with irregular, elongated margins, nearly reaching the anterior most point of the PM4 alveolus (Figure 7A). This characteristic is found in the genus *Microcavia* (Quintana 1996; Udrizar Sauthier 2020). The size of the recovered maxilla (length = 14.70 mm; width = 12.93 mm) indicates that it belongs to an extinct species larger than the extant *M. australis* (length = 10.41–11.49 mm; width = 9.63–10.40 mm). The molariforms have pear-shaped, cross-sections, with prisms (without interprism cement), labially convex and lingually pointed in the upper molars (M1 and M3), and conversely in the lower molars (PM4 and M1) (Figure 7B–E). These features match those of the genus *Microcavia* (Cabrera 1953; Contreras 1964; Quintana 1996).

The measurements obtained from the four molariforms fall within the range of values for the extinct species, particularly *M. robusta*, but clearly differ from *M. australis* (Supplementary Table S4; Figure 8). Notably, the M3 recovered exhibits a moderate external flexus, a long additional prism, and an additional flexus with parallel, deep, penetrating internal margins (Figure 7C). This feature is characteristic of *M. robusta*, distinguishing it from *M. criollensis*, in which the additional flexus of M3 has diverging and deep internal margins (Ubilla et al. 1999). Quintana (1996) noted a lack of intraspecific variation in the morphological pattern of M3 in the extinct species *M. robusta*. In contrast, there is considerable intraspecific morphological variation in extant

Microcavia species, particularly concerning some dental features, such as the size and shape of prisms and the flexus/flexids of the PM4/pm4 (Contreras 1964; Kraglievich 1930; Quintana 1996). The pm4 found at SPPL, with the poorly developed anterior prism extension delimited (Figure 7D), is similar to the pm4 of *M. robusta* illustrated by Quintana (1996: fig. 8E). Finally, the m1 displays a posterior prism slightly larger than the first ones, separated by a deep and oblique hypoflexid, with a fold on the lingual side (delimited by the internal flexid) that appears as a notch (Figure 7E). In summary, the measurements and morphological pattern of the specimens from SPPL allow us to assign these materials to *Microcavia* cf. *M. robusta*.

4.2 Zoogeographical and paleoenvironmental aspects

The discovery of the extinct *G. tixiensis* and *Microcavia* cf. *M. robusta* caviine rodents at SPPL (Guerrero Member of the Lujanian Formation - Late Pleistocene), is significant not only from a taxonomic point of view but also for its biogeographical and palaeocological implications. Notably, the levels containing specimens of *Galea* from SPPL are chronostratigraphically correlated with the oldest levels (~12,600 cal BP) of the nearby Campo Laborde archaeological site (Favier-Dubois et al. 2021; Prado et al. 2019), where a specimen of *G. leucoblephara* was found (Scheifler et al. 2015: fig. 3e). Additionally, *M. robusta* and *G. leucoblephara* are present in Lujanian sediments associated with the Last Glacial Maximum (LGM) at the Camet Norte paleontological site (southern coast of Buenos Aires) (Pardiñas et al. 1998; Figure 1). Moving toward the Holocene, several

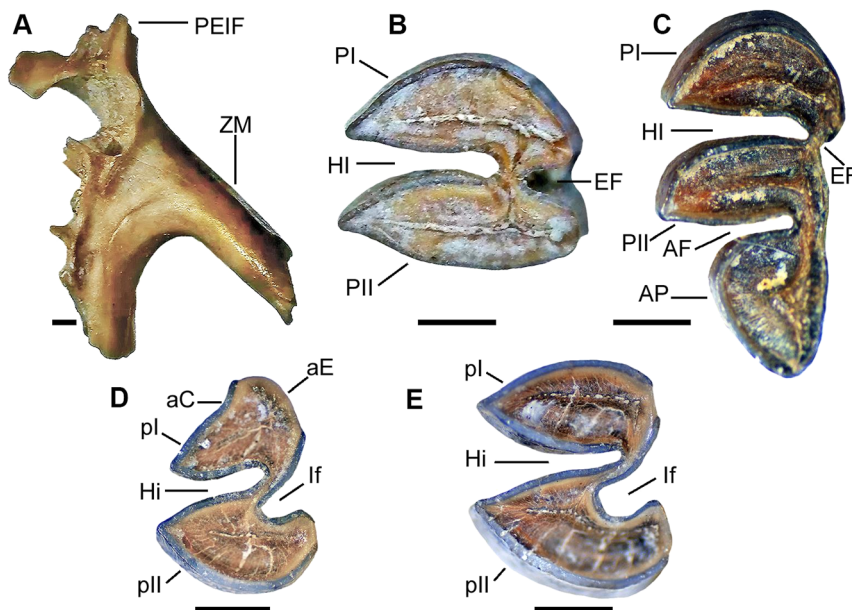


Figure 7: *Microcavia* cf. *M. robusta* specimens recovered from SPPL. (a) Left maxilla (FCS-P.324, U4-F7); (b) left upper M1 (FCS-P.328, U4-F9); (c) left upper M3 (FCS-P.325, U4-F7); (d) left lower pm4 (FCS-P.326, U4-F7); (e) left lower m1 (FCS-P.327, U4-F7). Abbreviations: aC, additional cleft; aE, additional extension; AF, additional flexus; AP, additional prism; EF, external flexus; HI, hypoflexus; Hi, hypoflexid; If, internal flexid; PI (upper) and pI (lower), anterior prism; PII (upper) and pII (lower), posterior prism; PEIF, Posterior edge of incisive foramina; ZM, zygomatic process of maxillary. Scales = 1 mm.

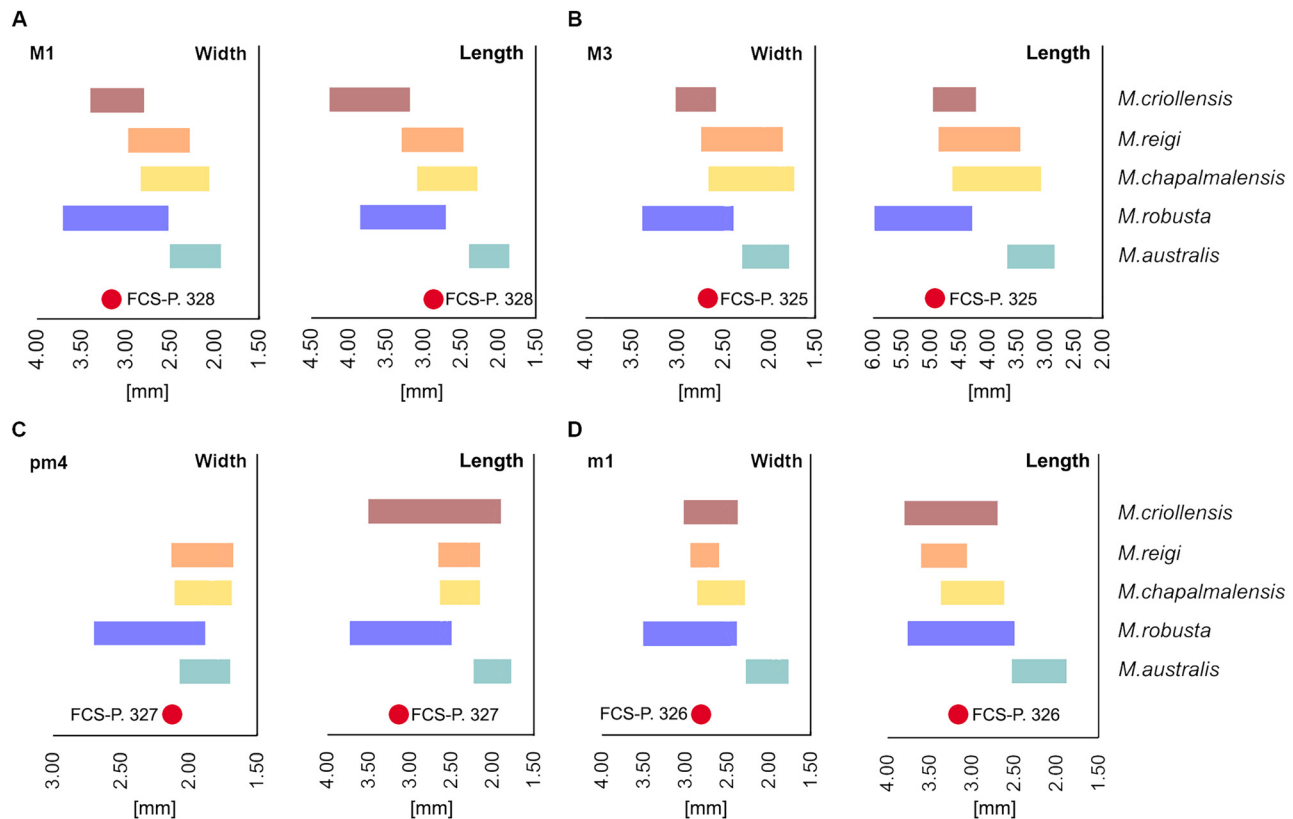


Figure 8: Ranges of maximum and minimum measurements of the M1, M3, pm4 and m1 molariforms from species of the genus *Microcavia*. Red dot corresponds to Salto de Piedra (FCS-P.328; FCS-P.325; FCS-P.327; FCS-P.326) specimens. (A) M1 width and length; (B) M3 width and length; (C) pm4 width and length; (D) m1 width and length.

fossil records of *G. leucoblephara* and *M. australis* are reported from the Pampasic Domain (e.g., Gómez and Bonomo 2019; Messineo and Scheifler 2016; Pardiñas 1999; Quintana 1996; Salemme 1990; Scheifler et al. 2012; Scheifler and Messineo 2016; Tonni 1985).

The living species of caviine rodents inhabiting nearby areas (*M. australis* and *G. leucoblephara*) are almost exclusively found in the arid and semi-arid environments of the Andean-Patagonian Subregion (*sensu* Ringuelet 1961) (e.g., Dunnum 2015; Teta et al. 2017). Both species reach the southern part of Buenos Aires Province (Figure 1), which coincides with the north-easternmost portion of the Patagonian Subregion (Ringuelet 1955). Even the subspecies *G. l. littoralis*, which mainly occurs in the northern part of the Patagonian Domain and the southern Subandean Domain, has its type locality in Bahía Blanca, located in the southern part of Buenos Aires Province (Figure 1; Dunnum 2015). However, the findings of *G. leucoblephara* and *M. australis* along the southeastern shore of Buenos Aires Province, suggest that both species (Figure 1; Fernández et al. 2012; Pardiñas and Cenizo 2023; Reig 1964) may have utilized coastal dunes as xeric corridors leading north. It appears

that the same corridor was also used by the sigmodontine rodents *Eligmodontia typus* and *Phyllotis* sp. during the arid and colder conditions, which prevailed in the Late Glacial Interval (LGI) (Pardiñas 1999; Pardiñas et al. 2010). Certainly, neither *Microcavia* nor *Galea* currently inhabit the typical grasslands of the interior of the Pampas phytogeographic unit, which almost entirely coincides with the Pampasic Domain, where SPPL is located.

The zoogeographic pattern of the Pampasic Domain (*sensu* Ringuelet 1955, 1961) during the Late Pleistocene differs significantly from the present-day pattern (e.g., Tonni 2025). During the Last Glacial Maximum (LGM), South America experienced the greatest extent of ice sheets favouring the presence of the characteristic open environments of the last glacial cycle (Clapperton 1993; Rabassa et al. 2022; Tonni 2025; Vivo and Carmignotto 2004). Unit 4 of SPPL (~16,300 to ~11,600 cal BP), which contains the faunal remains studied here, corresponds chronologically with the post-LGM deglaciation process and with the glacial readvance of the Antarctic Cold Reversal (ACR) (Rabassa et al. 2022; Tonni 2025). Various lines of evidence -isotopic, faunal, palynological, sedimentological- (e.g., Bonadonna

et al. 1999; Muhs and Zárate 2001; Prado and Alberdi 1999; Quattrocchio et al. 2008; Tonello and Prieto 2008, 2010; Tonni et al. 1999, 2003), suggest that the expansion of the landmass resulting from a lower sea level along the Atlantic coast was associated with more continental conditions, leading to a more arid climate and the expansion of shrubby environments in the Pampas during the Late Pleistocene (~16,000 to ~11,700 BP). The mammalian taxonomic structure of the Pampasic Domain changed abruptly after the end of the LGM, particularly after the late glacial expansion of the ACR, when all megamammals and most species of large mammals went extinct (e.g., Cione et al. 2009, 2011). Although the significant climate changes and, possibly, the arrival of the first humans primarily affected the larger species (e.g., Cione et al. 2009; Prates and Perez 2021), some smaller species also became extinct (e.g., Pardiñas 1999; Quintana 1996, 1998; Teta et al. 2014).

During the Late Pleistocene, *M. australis* and *M. robusta* coexisted in most of the Pampasic Domain (Brambilla et al. 2021; Quintana 1996). The former has retreated to the west and south, avoiding the increasing humidity during the Holocene in the Pampasic Domain. The latter species was recorded in the southeastern and northern Pampean region, becoming extinct at the Pleistocene-Holocene boundary (Brambilla et al. 2021; Quintana 1996). The fossil records of these caviines at SPPL are located more than 250 km northeast of the current geographic distribution of the living species from these genera. Additionally, the extinct *G. tixiensis*, besides being found at SPPL and CT, also has a Late Pleistocene (Lujanian age) fossil record in Arroyo Toropí, located in Corrientes Province (Francia et al. 2012), within the Subtropical Domain, approximately 250 km northeast of the Pampasic Domain and 210 km east of the current distribution of *G. leucoblephara* (Figure 1). The loss of caviine diversity in the Pampasic Domain is evident since the Late Pleistocene-Holocene transition, where four species were recorded, to the Early Holocene and historical times, when *G. tixiensis* and *Cavia aperea* coexisted, at least in the Tandilia system (e.g., Quintana 1996, 1998, 2001). *G. tixiensis* appears to have become extinct in the 19th century, likely due to the negative effects of exotic livestock and intensive agriculture (Teta et al. 2014).

Another species of *Galea* could be added to the list of caviines from the Late Pleistocene of the Pampas if we consider the records of *G. ortodonta* in the grasslands on the northern bank of the Río de la Plata in southern Uruguay (Figure 1; Ubilla and Rinderknecht 2001, 2014). Conversely, *M. criollensis*, associated with the same period (Lujanian age), was found in the Sopas Formation (northern Uruguay, Figure 1), outside the Pampas grassland (Quintana 1996; Ubilla et al. 1999).

Currently, the Subtropical species *C. aperea* Erxleben, 1777 is the only caviine inhabiting the grasslands of the Pampasic Domain area in Buenos Aires Province, reaching Bahía Blanca (Cabrera 1953; Dunnum 2015; Massoia 1973). Even the Subtropical large caviid *Hydrochoerus hydrochaeris* (Linnaeus, 1766) continues its migration north-south, as evidenced by recent records in southern Buenos Aires Province near Bahía Blanca (Doumecq Milieu et al. 2021). In the southern part of Buenos Aires Province, we find the boundary between the Patagonian and Subtropical mammal faunas (Fernández et al. 2012), marking the presence of greater diversity in caviine rodents (*C. aperea*, *G. leucoblephara*, and *M. australis*).

Finally, Holocene mammal communities of the Pampasic Domain have become well adapted to the grassland environments and warmer, wetter conditions, which peaked during the Holocene Climatic Optimum (HCO, 7,500-4,500 BP) and the Medieval Climatic Anomaly (MCA, 800-1,300 AD). This period saw the northward expansion of subtropical species, such as the sigmodontine rodents *Bibimys* cf. *B. torresi*, *Pseudoryzomys simplex*, and *Scapteromys aquaticus* (García-Morato et al. 2021; Pardiñas 1999, 2000; Pardiñas et al. 2010; Tonni 2025; Tonni et al. 1988).

5 Conclusions

- (1) *Galea tixiensis* morphometric comparisons with specimens from its type locality (Cueva Tixi), confirm the taxonomic status of this caviine rodent as a distinct species.
- (2) The expanded original description of the mandible and lower premolar of *G. tixiensis*, provided in this study, is particularly noteworthy.
- (3) The presence of this caviine in Salto de Piedra expands its chronological framework to approximately 16,300 years BP, which is 5,000 years earlier than previously recorded, and its distribution range by about 200 km further east within the Pampasic Domain.
- (4) The discovery of the extinct *G. tixiensis* and *Microcavia* cf. *M. robusta* caviine rodents at Salto de Piedra (Guerrero Member of the Lujanian Formation, ~16,300-11,700 cal BP), along with other species recorded in different localities (*M. australis*, *G. leucoblephara* and *G. ortodonta*), suggests a greater diversity of caviine rodents during the Late Pleistocene in the Pampasic Domain compared to later periods.
- (5) With rising temperatures and humidity during the Holocene, and the gradual replacement of shrub steppes by grasslands, *M. robusta* and *G. ortodonta* became extinct, while *C. aperea* arrived from the north. This latter

species is now the only caviine rodent inhabiting the typical grasslands of the Pampasic Domain.

- (6) The higher diversity of caviid rodents in the Late Pleistocene of the Pampasic Domain is comparable to the current situation in the southern region of Buenos Aires Province. Here, the transition zone between Patagonian and subtropical mammal fauna results in a higher diversity of caviine rodents (*C. aperea*, *G. leucoblephara*, and *M. australis*). This suggests that the greater diversity of caviine rodents observed during the Late Pleistocene could be associated with the displacement of the Pampean/Patagonian ecotone into more interior areas of the Pampasic Domain.
- (7) During the Holocene, *M. australis* and *G. leucoblephara* were restricted to southern coastal environments, while *G. tixiensis* apparently became extinct in the 19th century, likely due to the negative impacts of exotic livestock and intensive agriculture.

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